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RED BREASTS AS HONEST SIGNALS OF MIGRATORY QUALITY IN A LONG-DISTANCE MIGRANT, THE BAR-TAILED GODWIT[1]

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Abstract. Bar-tailed Godwits (*Limosa lapponica*) partially molt contour feathers before flying to their subarctic breeding grounds. This molt starts in February on the West African wintering grounds, is suspended in late April before the flight to the staging sites in western Europe, and is continued by more than half of the birds during their stage in May in the Dutch Wadden Sea. During molt the appearance of the plumage changes from the dull grey of a winter plumage to an intense rusty-red in males and a beige-rufous in females with a complete breeding plumage. The total mass of the plumage remains the same. Molt is scheduled earlier and is more intense in males than in females. The duration of contour feather growth on the Dutch staging area is estimated to be 12 days, leading to an estimated daily dry feather production of 0.09–0.13 g/day. On the Dutch staging area molting individuals of either sex had a more complete breeding plumage than non-molting birds and were always heavier. Very few birds started molt in the last 12 days before northward departure indicating that time provides a critical constraint on the occurrence of molt. Although the extra costs of molt are estimated at only 7% of the costs of the simultaneous energy storage, the site-related difference in the mass of molting individuals suggests that the decision to molt depends also on nutritional factors. We argue that in view of the tight time/energy schedules faced by these long-distance migrant godwits, only individuals which have sufficient energy/nutrient reserves for the time of the year due to better feeding or flying performances, can afford to upgrade their plumage on the staging areas. The extent and quality of the breeding plumage could thus provide males as well as females with an indicator of the migratory, and possible concomitant, qualities of potential mates.

Key-words: Migration; molt; energy; nutrition; storage; stopover ecology; mate choice; honest signals; sexual selection.

INTRODUCTION

Bar-tailed Godwits (*Limosa lapponica*) breed on dwarf shrub and forest tundra from northern Scandinavia across subarctic Siberia to western Alaska. Here, the summer season is short and breeding schedules tight. Siberian-breeding Bar-tailed Godwits winter in the West African tropics, 8,000–10,000 km away, and their afro-arctic travels occupy more than three months each year (Cramp and Simmons 1983, Drent and Piersma 1990). This way of life is typical for many migrating shorebird species and puts high demands on a proper timing of molt, energy storage, migratory flights and reproduction (Ens et al. 1990). Tight annual schedules imply that timing delays during any one activity easily affect reproductive performance, even if such delays are incurred half a world away (Piersma 1987). Interspecific comparison of migration distance and parental care and mating systems in sandpipers (Myers 1981) gives further suggestions for the qualitative effects of migration on breeding biology.

Among shorebirds, most sandpipers (Scolopacidae) and several plovers (Charadriidae) have a breeding plumage which is distinct from, and often more colorful than, the plumage carried the rest of the year (Cramp and Simmons 1983, Hayman et al. 1986). In addition, there are sex and age differences in the color and quality of the breeding plumage. Such differences have been shown to affect pairing and mate choice (Edwards 1982, Höglund et al. 1990). Bar-tailed

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TABLE 1. Sex ratios ($n_{males}/n_{females}$) of Siberian-breeding Bar-tailed Godwits on their West African wintering and Dutch and German spring staging grounds as estimated with various techniques. *n* refers to the number of examined individual godwits. "Wilster-netting" is a historical Dutch method of catching Greater Golden Plovers *Pluvialis apricaria* (Koopman and Hulscher 1979). Sources are: (1) Zwarts 1988, p. 49; (2) Piersma 1982, Table 8.4; (3) Zwarts & Piersma 1990, Table 1 (sex ratios); (4) Zwarts et al. 1990a, Figure 3 (*n*-values); (5) Piersma & Jukema 1990, Table 3; (6) this study, Figure 7; (7) Prokosch 1988, Table 26.

Location	Lat.	Period	Sex ratio	*n*	Method	Source
Guinea-Bissau	11°N	Dec–Feb	1.07	?	Field scans	(1)
Mauritania	20°N	February	2.32	256	Field scans	(2)
		March	4.24	4,411	Field scans	(3, 4)
		April	2.58	5,712	Field scans	(3, 4)
		March–April	2.50	70	Mist-netting	(5)
Netherlands						
Frisian coast	53°N	May	2.10	842	Wilster-netting	(5)
Texel	53°N	18–22 May	1.11	77	Wilster-netting	(6)
Germany	55°N	May	0.79	337	Cannon-netting	(7)

Godwits are strongly sexually dimorphic, both with respect to size (the ratios, male-to-female, of average wing, tarsus and bill lengths are 0.94, 0.94 and 0.82, respectively; Cramp and Simmons 1983) as well as to breeding plumage color (males usually attaining a more intense rusty-red breast and belly than females). Although Bar-tailed Godwits are monogamous and have biparental care (I. Byrkjedal, pers. comm.), the consistent predominance of males on the main wintering area in Mauritania and perhaps also on the European spring staging sites (Table 1) offers the possibility that there is severe competition among males for mates if such sex ratios are maintained onto the breeding grounds (Byrkjedal et al. 1989 give detailed descriptions of the sexual behaviors involved). If the color or quality of the males' nuptial plumage influences mate choice decisions by females, the extent (affecting plumage color) and recency (affecting plumage quality) of the molt into the red breeding plumage may be important during pair formation (e.g., Andersson 1982, 1983).

It is arguable whether molt is a costly process (King 1981, Murphy and King 1991), but it does generally require sufficient nutritional investments or give functional impairments to be often separated in time from other important activities such as breeding (Murton and Westwood 1977). The cost of the partial molt from a winter into a breeding plumage as carried out by many shorebirds in spring has never been quantified. That shorebirds may molt while also depositing the nutrient stores for long-distance flights (Koopman 1986, Zwarts et al. 1990c), suggests that molting and gaining body mass are compatible.

We studied Bar-tailed Godwits on their West African wintering grounds in Mauritania before their northward migration and on their main European staging area, the Wadden Sea, in The Netherlands. The overlapping biometrics, the close fit between the timing of northward departure from Mauritania and arrival in the Wadden Sea, and the within-spring resightings of Mauritania-marked individuals in the Dutch Wadden Sea, led Piersma and Jukema (1990) to suggest that these birds are from one population. This paper describes in detail the pre-nuptial molt of Bar-tailed Godwits and analyzes it in relation to plumage color, nutritional status, and migration schedule. The analysis suggests links between molting during long-distance migration and breeding performance.

METHODS

FIELDWORK

Bar-tailed Godwits were captured in late March and April 1985 and 1986 on the Banc d'Arguin in Mauritania, West Africa (19°53′N, 16°17′W), in April–May 1984–1990 on a staging site along the Frisian coast in the eastern Dutch Wadden Sea (53°21′N, 06°06′E), and from 18–22 May 1992 in meadowland near Den Burg on the island of Texel in the western Dutch Wadden Sea (53°03′N, 04°48′E). Details of capture methods, biometrics and migration phenology are presented by Piersma and Jukema (1990). Very few godwits younger than three years of age were captured on the Dutch staging sites and only fully

TABLE 2. Summary of the various plumage and molt variables used to describe the acquisition of a breeding plumage by Bar-tailed Godwits in Mauritania and The Netherlands during northward migration. Variables 2 and 5 are further explained in Figure 1. Variables 1 and 6 were scored at all study sites, but the remaining ones only for godwits captured in the Dutch Wadden Sea. Variables 4 and 7 were registered in a sample of catching casualties only.

Variable	Name of score	Level of measurement	Scale
1. Extent of breeding plumage	Plumage score	Ordinal	7 points
2. Composition of breast plumage	Feather type	Nominal	3 points
3. Color of breeding plumage feather	Breeding feather color	Ordinal	5 points
4. Intensity of breast & belly molt	Molt intensity	Ordinal	4 points
5. Stage of completion of molting breast feathers	Molt phase	Ordinal	5 points
6. Presence or absence of molt	Yes or no	Nominal	2 points
7. Dry contour feather mass	"Dorsal" feather mass "Ventral" feather mass	Continuous	

adult birds (>3rd calendar year) are examined here.

Upon capture birds were banded, three linear dimensions (wing, bill and tarsus + toe length) were taken, and they were weighed to the nearest gram. Subsequently, a series of seven variables of various aspects of plumage and molt (Table 2) was recorded from all captured birds or samples of captured or accidentally killed godwits. Because none of the birds showed flight feather molt, only contour feathers play a role in this study.

On the Banc d'Arguin and in the Dutch Wadden Sea the extent of breeding plumage was evaluated on the basis of the color of back, breast and belly, and was scored on a seven-point scale (1 = winter plumage, 2 = trace of breeding plumage, 3 = ¼ breeding plumage, 4 = ½ breeding plumage, 5 = ¾ breeding plumage, 6 = trace of winter, and 7 = full breeding plumage). From most godwits captured on the Frisian coast in 1986–1990, a small sample of about 10 breast feathers was plucked (see Jukema and Piersma 1987 and Fig. 1). Subsequently, the feathers were assigned to three categories (Fig. 1): (1) winter type (almost white), (2) striped feather type (black bars on a white to rosy background), and (3) red breeding plumage feather type (evenly rusty-red). In addition, we recorded whether feathers showed waxy sheaths at their base and were thus growing. Based on a series of reference feathers, the color of the breeding plumage feathers in the samples was scored on an arbitrary scale of an increasingly intense red color, ranging from 1 = light rufous to 5 = dark rusty-red. In a sample of staging birds from the Dutch Wadden Sea accidentally killed during catching, molt intensity (the relative density of growing feathers) on the breast was scored on a four point scale where 0 = no molt, 1 = light molt, 2 = medium molt and 3 = heavy molt.

The staging birds in the Dutch Wadden Sea which showed contour feather molt did so in a rather simultaneous fashion. Therefore, molt *phase* instead of molt *intensity* was scored on a five point scale (illustrated in Fig. 1) where 0 = no molt, 1 = feathers in pin, 2 = feathers are ¼ grown, 3 = feathers half-grown, 4 = feathers ¾ grown and 5 = new feathers (i.e., the scoring system illustrated by Ginn and Melville 1983). In the Dutch Wadden Sea, molt phases 0 and 5 were distinguished by the traces of waxy sheaths sometimes still present in the plumage of birds with recently completed feather growth and the slightly brighter color of the newest cohort of contour feathers compared to those grown earlier in West Africa. Errors made here would decrease, rather than increase, the observed differences between categories.

FEATHER WEIGHINGS AND COUNTS

To document the mass of contour feathers replaced in spring we plucked and weighed all flight and contour feathers in a sample of godwits accidentally killed during the catching operations. Feathers of the undertail, belly, breast, neck and head (the 'ventral' feathers, which are all reddish in a full breeding plumage) were collected sep-

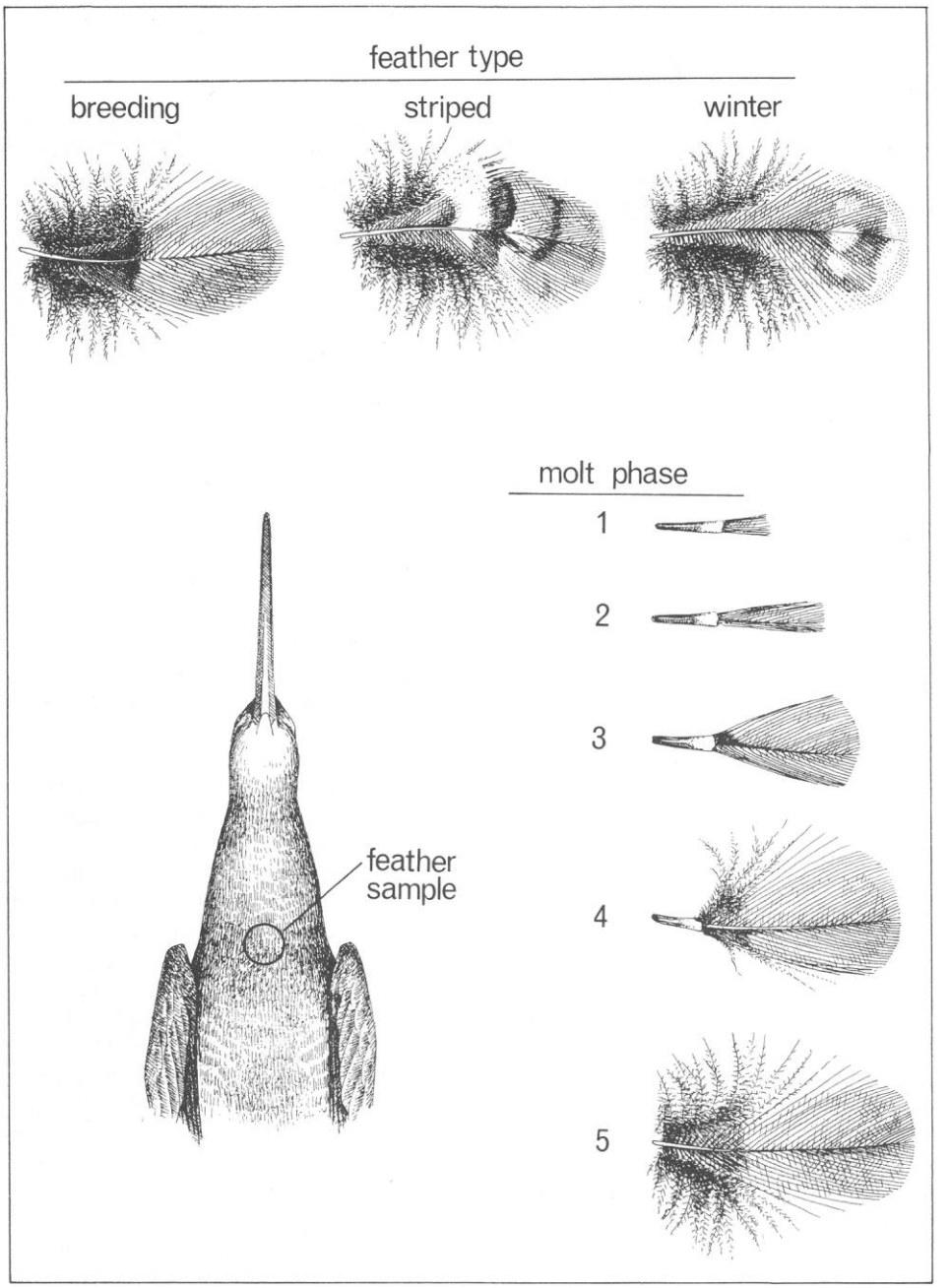

FIGURE 1. Categorization of breast feather types and their molt phases, and the location on a Bar-tailed Godwit where a feather sample was plucked. A full-grown breast feather is 2.5–3 cm long. (Feather drawings by Ruurd Noordhuis.)

arately from the feathers of the uppertail, back, the scapulars and wing coverts (jointly called the 'dorsal' feathers). Both samples were weighed after drying to constant mass at 60°C. Numbers of contour feathers were estimated for six birds (three of either sex, with different molt intensity scores), treating the dorsal and ventral feathers separately. Feathers were counted in five subsamples for each bird weighing 0.161 g on average for 'dorsal' and 0.099 g for 'ventral' feathers. The numbers of growing feathers in these five samples were registered and their percentages with respect to the totals (averaging 284 feathers in 'dorsal' samples and 386 in 'ventral' samples of the different birds) calculated. The total number of feathers was calculated by adding 50 flight (20 primaries, 20 secondaries and 10 tertials) and 12 tail feathers to the estimated total number of contour feathers.

STATISTICS

Calculation of means, standard deviations, and analyses of variance were carried out in Lotus-123 and SPSS-X. Box-plots were made with SYSTAT. To meet criteria for data-distributions in analyses of variance, the intervals between plumage scores were made equal by taking together scores 1 and 2 as score 2, and scores 6 and 7 as score 6.

To examine the probability of molt status being conditional upon sex, site of capture and body mass, we used logistic regression models, a category of generalized linear models (Nelder & Wedderburn 1972, McCullagh & Nelder 1989). These models fit a logistic curve through binomially distributed data in the form:

$$p(y = 1) = \exp(lp)/(1 + \exp(lp)).$$

$p(y = 1)$ is the probability of an individual godwit to be in molt and lp (linear predictor) is analogous to a standard regression equation, i.e. the sum of a constant and the effects of independent factors (in our case sex, site and mass) and their interactions. Different models were evaluated on the basis of the deviance (D), which is proportional to the log of the ratio of the likelihood achievable for the full model and that achieved by the model under consideration:

$$D = \log(L_{\text{full model}}/L_{\text{model under investigation}}).$$

A full model is an exact fit and it contains as many parameters as there are observations. Its deviance is thus zero. The null model is the simplest version and has just one parameter, representing a common constant p for all observations. If the two models are compared, the difference in deviance (G^2) is approximately χ^2_v distributed under the hypothesis that the simplest model is true. Here v is the difference in the number of degrees-of-freedom. Likelihood-ratio chi-square tests may therefore be used to test the significance of improvement of a model if a new parameter is added. Maximum likelihood estimates of the parameters in the logistic regression models were made using the statistical package GENSTAT 5 (Payne et al. 1987).

RESULTS

TIMING AND EXTENT OF MOLT INTO A BREEDING PLUMAGE

Bar-tailed Godwits start the partial molt of contour feathers into a red breeding plumage on their wintering grounds in late February–early March (Zwarts et al. 1990b, 1990c), the males attaining an average plumage score of 4.4 points out of 7 by early April (Fig. 2). Between 11 and 18 April, many males stopped contour feather molt. Those doing so had a more complete breeding plumage than those that were continuing (average plumage scores of 5.1 and 4.7, respectively, Fig 2). We were unable to collect adequate data on males after 18 April, and on females throughout the study period on the Banc d'Arguin.

The average departure date of male Bar-tailed Godwits from the Banc d'Arguin for their flight to western Europe is 25 April. The average arrival date at our study site on the Frisian Wadden Sea coast is 29 April (Piersma and Jukema 1990). The extent of breeding plumage of males scored just after arrival (Fig. 2) equalled that attained by non-molting (and presumably 'ready'; Zwarts et al. 1990c) birds on the Banc d'Arguin before departure (average plumage scores of 5.0 and 5.1 respectively). This suggests that godwits do not actively molt during and just after this migratory flight. This is confirmed by the finding that during the arrival period in the Wadden Sea (27 April–5 May) few males (3 out of 72) and none of the 33 females showed active contour feather molt (Fig. 3).

In the period 6–10 May, 14.5% of the males had started molt but only 1.6% of the females had started (Fig. 3). During the rest of the month, 71% of males and 62% of females showed active contour feather molt. The males were always in a more advanced phase than the females. That

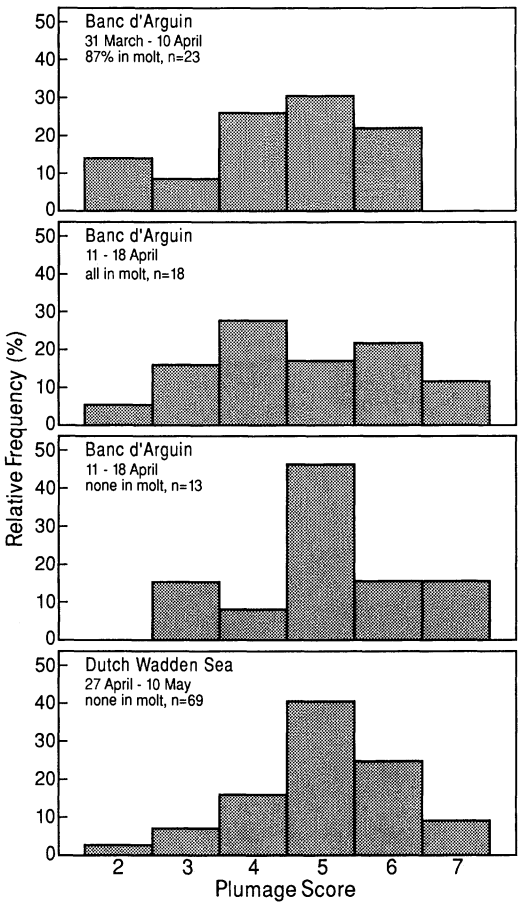

FIGURE 2. Temporal changes in the distribution of breeding plumage scores in male Bar-tailed Godwits on the Banc d'Arguin, Mauritania, in April (three upper panels), in comparison with the distribution of plumage scores upon their arrival in The Netherlands (lowest panel). The time axis is from top to bottom here, whereas it is from left to right in the following equivalent figure.

males have the lead over females in the timing of molt conforms with their earlier migration to and away from the Wadden Sea staging area (Prokosch 1988, Piersma and Jukema 1990). Although few godwits were captured in the period of departure from the Wadden Sea to Siberia (31 May and 1 June are average departure dates for different years; Piersma and Jukema 1990), it is likely that birds do not take off on migratory flights with active body molt. Of the eight males captured from 29–31 May, only three showed active molt and these were somewhat lighter (365 g) than those that showed no molt (377 g) and were therefore likely to also leave somewhat later (after first finishing molt). The two females captured then showed no active contour feather molt.

The presence of molting birds in the godwit population staging along the Frisian coast did not lead to significant changes in plumage scores in males (Fig. 3; one-way ANOVA, $F_{3,453} = 0.61$, $P = 0.61$). In females also, average plumage scores did not differ significantly between periods ($F_{3,232} = 1.31$, $P = 0.27$). Although the godwit population of the Frisian coast is rather closed, with little immigration after the arrival period 27 April–5 May (Piersma and Jukema 1990), the increase in the proportion of females with a less-complete breeding plumage after 5 May suggest that a number of unmolted birds arrive between 5 and 10 May.

The larger effect on the average plumage color of the population by a smaller proportion of molting individuals in females compared to males is explained by the differences in the type of feathers replaced during the partial molt on the staging site (Fig. 3, lower panels). Upon arrival in the Wadden Sea, males carried few winter feathers. Primarily, striped feathers were replaced by the red breeding plumage feathers. In females, however, it was the remaining winter feathers that were replaced by breeding plumage feathers. Since winter feathers are whiter than the often rosy-colored striped feathers, the plumage color of females was more affected by the molt than the plumage color of males.

The lighter color of the breeding feathers of females compared to males was confirmed by the normally distributed color scores. The color score of 78 males averaged 3.72 (SD = 0.80) and of 31 females averaged 2.23 (SD = 0.92); a significant difference (Student's t-test, $t = 7.9$, $P < 0.05$). There were no significant differences between the colors of breeding feathers of birds with different plumage scores, nor between actively molting and non-molting birds of either sex (ANOVA, $P > 0.05$).

DURATION OF MOLT IN DUTCH WADDEN SEA

The molt of contour feathers during the staging period in the Dutch Wadden Sea is simultaneous; all molting feathers do so at the same time and are thus in the same phase. This makes it relatively straightforward to estimate the duration of the growth period of these feathers. Mindful of the provisos of Underhill and Zucchini (1988)

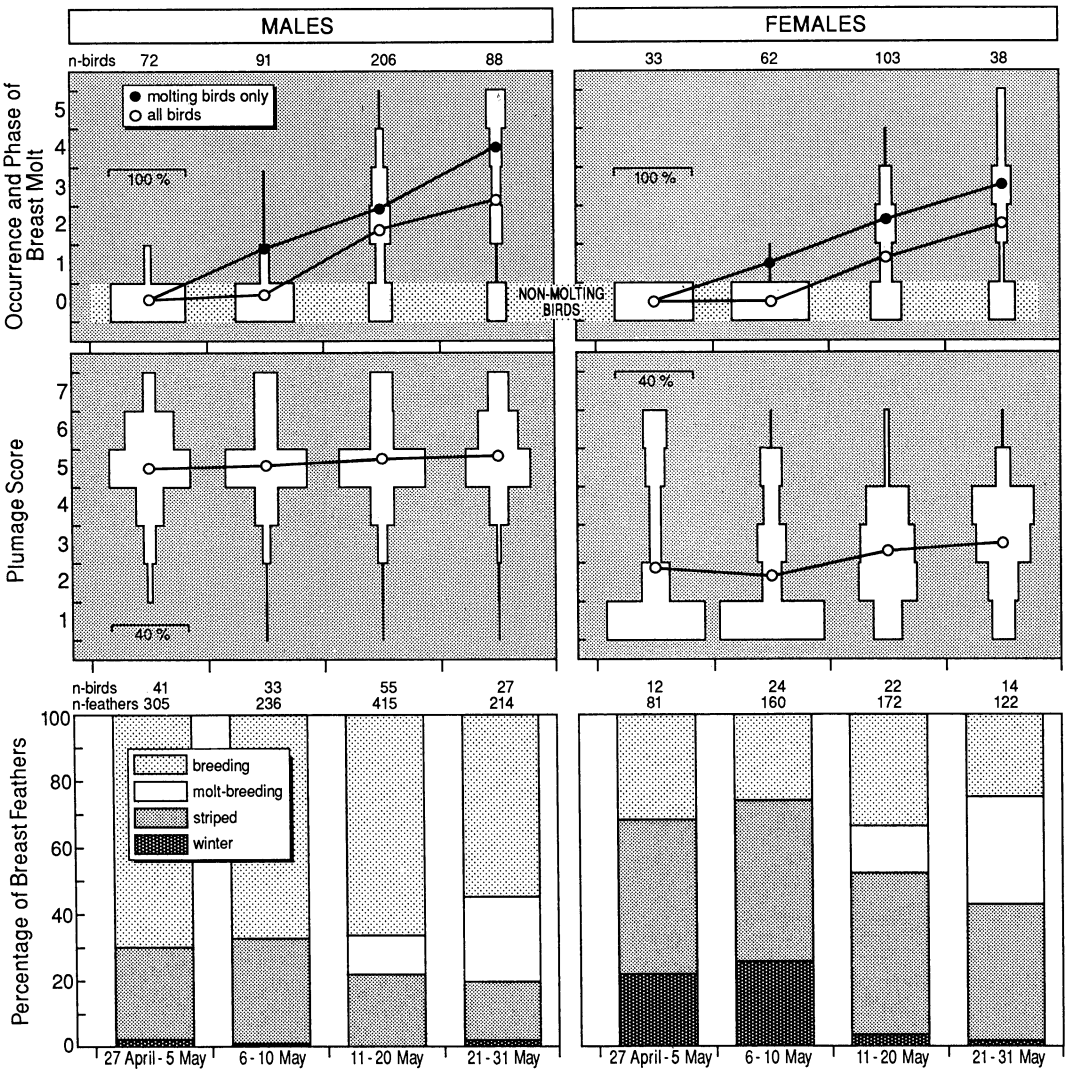

FIGURE 3. Temporal changes in the distribution and averages in the phase of breast feather molt (top panels), plumage score (mid panels) and the composition of sampled breast feathers (low panels) in Bar-tailed Godwits during their stopover in May in the Dutch Wadden Sea. Period, sex and category specific averages are indicated by opened and filled circles.

and Underhill et al. (1990), we followed the first few actively molting individuals through molt (taking these as a uniform 'cohort'). We derived a somewhat crude estimate of molt duration by regressing the active molt phases (scores 1–4) of the first and fifth encountered male and female (the latter representing the median of the first nine birds in the respective molt phases) on date and extrapolating to molt phase 5 (Fig. 4). This yields reasonably consistent estimates of 15.1 and 11.5 days in females, and 11.8 and 9.3 days in males, and an overall average of about 12 days.

QUANTITY OF FEATHERS REPLACED

To estimate the nutritional requirements of the spring molt, we determined feather quantity. Six Bar-tailed Godwits carried an average of 2,201 (SD = 209) dorsal feathers, 3,577 (SD = 564) ventral feathers and 5,841 (SD = 653) contour and flight feathers (Table 3). In males molting in

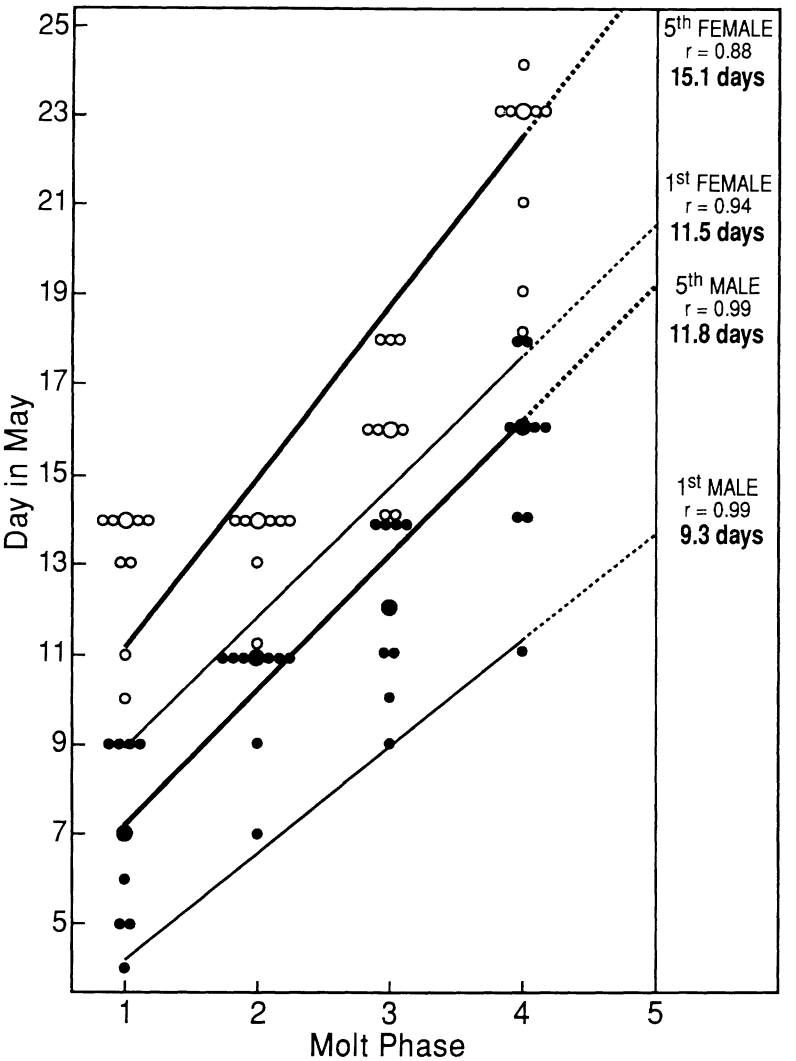

FIGURE 4. A simple method to estimate the duration of the simultaneous breast feather molt of Bar-tailed Godwits during their stay in May in the Dutch Wadden Sea is a plot of the date of capture of the first 'cohort' individuals of either sex in the respective molt phases 1–4 on molt phase and then linearly extrapolating to feather completion (molt phase 5). By regressing molt phase on date (note that this is x on y, see text) of the first and the fifth (i.e., median value of nine) individual in each molt phase and then extrapolating to molt phase 5, we get four estimates of molt duration as indicated by the figures in the column at right. Males are given by closed dots and females by open circles; the medians are indicated with fatter symbols.

the Dutch Wadden Sea 4–9% of the dorsal feathers and 20–24% of the ventral feathers were being replaced. In molting females, these values were, respectively, 2% and 14%. There were no differences between molt intensity scores 1 (light) and 2 (medium) in the four (two of each sex) examined birds of each category.

There were no differences in contour feather mass in relation to plumage score, either in males (one-way ANOVA, $F_{2,37} = 1.31$, P 0.28) or in females ($F_{2,18} = 0.28$, $P = 0.76$) (Fig. 5). Assuming that half of the dorsal plumage and the entire ventral plumage is replaced during the pre-nuptial molt, males would produce 6.54 g dry feather mass and females 8.00 g. Only part of this will be produced in the Wadden Sea area in May. Based on values in Table 3 and average dry feather masses, the average dry mass of contour feath-

TABLE 3. Numbers of feathers and percentage of feathers in growth in six Bar-tailed Godwits of different sex and molt intensity. All were in almost complete breeding plumage (score = 6 in males, score = 5 in females). "Dorsal" stands for the uppertail and back feathers, scapulars and wing coverts, while "ventral" stands for the undertail, belly, breast, neck and head feathers. The total refers to all feathers, including the flight feathers.

	Molt intensity score					
	0		1		2	
	Average (SD)	%-grow	Average (SD)	%-grow	Average (SD)	%-grow
Males						
Dorsal	2,038 (411)	0%	2,437 (392)	9.1%	2,293 (489)	4.4%
Ventral	4,145 (743)	0%	3,476 (568)	23.9%	3,903 (739)	20.5%
Total	6,245 (948)		5,975 (835)		6,258 (1,015)	
Females						
Dorsal	1,976 (436)	0%	2,037 (353)	2.4%	2,426 (470)	2.2%
Ventral	2,521 (279)	0.5%	3,703 (509)	14.6%	3,716 (362)	14.0%
Total	4,559 (492)		5,802 (467)		6,204 (419)	

ers grown during the staging period in the Wadden Sea is 1.53 g in males and 1.11 g in females.

DIFFERENCES BETWEEN MOLTING AND NON-MOLTING BIRDS

Why do some Bar-tailed Godwits show body molt while staging in the Wadden Sea and others do not (Fig. 3)? We tested the possibility that only the godwits with incomplete breeding plumages showed partial molt on the staging site to complete the feather replacement started in West Africa. However, in both males and females, the molting individuals had more complete breeding plumages than the non-molting birds (Fig. 6). Although we examined other parameters such as body size, the only statistically significant difference between the molting and non-molting categories was in date-specific body mass. For both sexes and in all periods for which comparisons can be made, molting birds were heavier than non-molting birds (Fig. 6).

In females, but not males, arriving birds (i.e., from the period 27 April–5 May) with a less complete breeding plumage (score 3 or less) were lighter than birds with a more complete breeding plumage (score 4–7). Their body masses were, respectively, 282 g (SD = 26, $n = 24$) and 313 g (SD = 38, $n = 9$) (two-tailed Student's t-test, $t = 2.26$, $P = 0.05$). In no other period were there significant differences between body masses of birds in different plumage categories (ANOVA, $P > 0.05$).

Instead of examining a time series of godwits, it is also possible to compare the plumage and mass characteristics of molting and non-molting birds from a single period. A sample of 98 godwits from Texel during the period 18–22 May 1992 was compared with the 143 godwits captured along the Frisian coast (a straight-line distance of 97 km) at the same time of the year (Fig. 7). There is a significant effect of body mass on the probability of being in molt (Table 4) and the mass function differs between males and females. In addition, there is an effect in both sexes

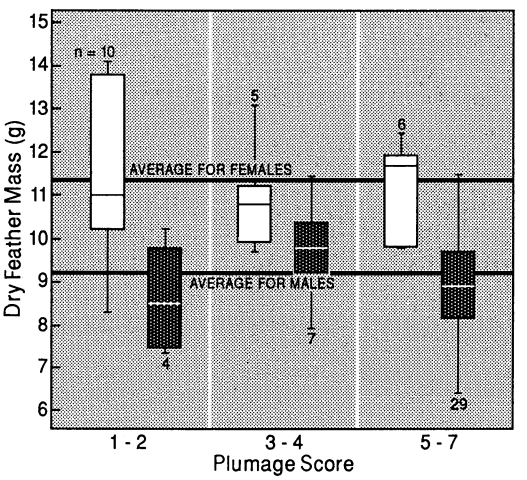

FIGURE 5. Dry contour feather mass of different plumage categories in male (shaded box) and female (open box) Bar-tailed Godwits from the Dutch spring staging areas. For each plumage and sex category the vertical line indicates the range in values, the three layers of the box giving the division in quartiles. Thus 25% of the values are found below the box and 25% above the box, with the midline indicating the median (50% below and above). There is no change in dry contour feather mass with an increase in breeding plumage.

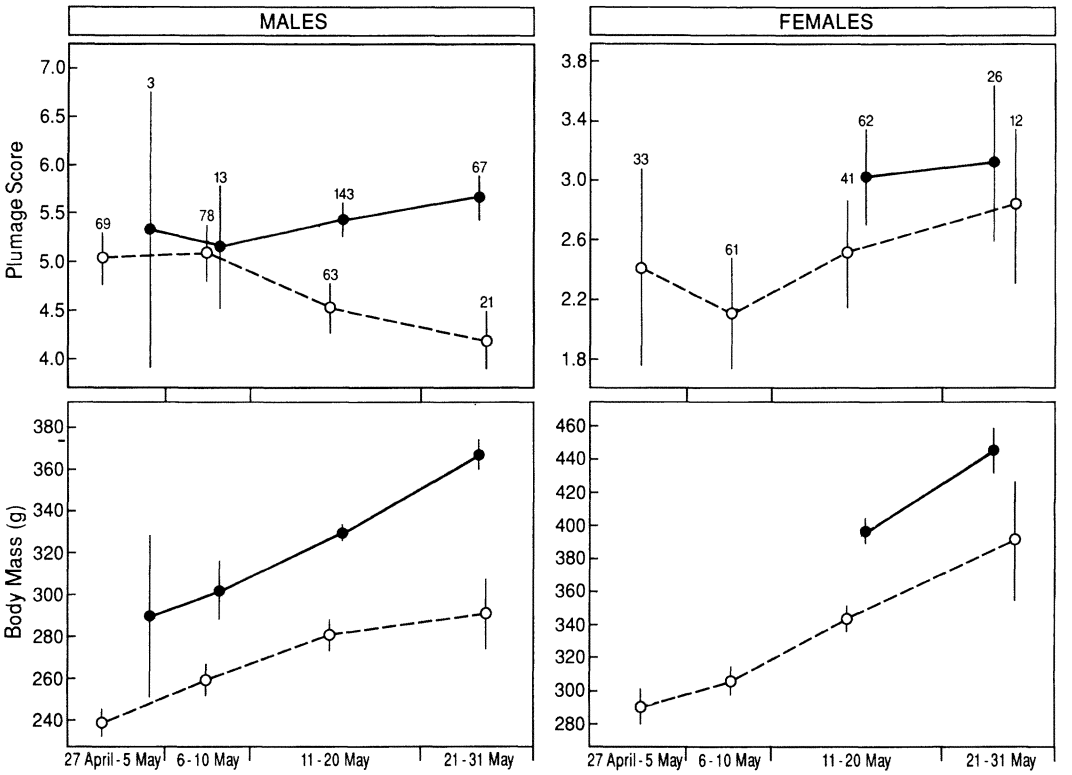

FIGURE 6. Temporal changes in average plumage score (top panels) and body mass (lower panels) of Bar-tailed Godwits during their stopover period along the Frisian coast in May differentiating between those that restart contour feather molt (closed dots) and those that do not (open circles). Averages with 95%-confidence intervals and *n*-values are presented. The differences between periods in plumages score were only significant for non-molting males (ANOVA, $F_{3,227} = 5.26$, $P = 0.002$). The difference in body mass between periods were significant (ANOVA's, $P < 0.001$) for all categories. The differences in plumage score between the molting and non-molting categories were significant for the third and fourth periods in males, and only the third period in females (ANOVA, $P < 0.01$). The differences in body mass between the molting and non-molting categories were significant for all periods in males, and for the last two periods in females (ANOVA's, $P < 0.01$).

of catching site on the mass-related probability of being in molt (Table 4, Fig. 7). Despite all birds on Texel being lighter (292 ± 64 g for males and 371 ± 63 g for females) than along the Frisian coast (335 ± 36 g for males and 402 ± 48 g for females), molting godwits were heaviest on Texel. This is not due to site-specific variations in body size; in either sex, wing, bill and tarsus + toe length did not differ significantly; Student's *t*-test, $P > 0.05$).

DISCUSSION

IS GAINING MASS COMPATIBLE WITH MOLT?

That among Bar-tailed Godwits staging in the Dutch Wadden Sea molting birds were consistently heavier than non-molting individuals contrasts with the general finding that molting shorebirds are lighter than non-molting ones (Ens et al. 1990, Zwarts et al. 1990c). The negative correlation between body mass and the occurrence of body or wing molt has variously been interpreted as 1) indicating the high nutritional cost of molt (Hanson 1962), 2) an adaptation to enhance flight capabilities in cases where flight feather molt occurs simultaneously with contour feather molt (Boere 1976), 3) an inability to simultaneously molt and fly long-distances (Koopman 1986, Zwarts et al. 1990c), and 4) the occurrence of molt at a time of the year when food is relatively abundant and no strategic nutrient stores need be carried (Masman and Daan 1987). None of these studies was, however, exclusively concerned with birds on staging areas that are

probably time-stressed, especially in spring (Alerstam and Lindström 1990, Gudmundsson et al. 1991). In Ruffs *Philomachus pugnax,* the last males to leave the post-breeding staging grounds in The Netherlands for the African wintering areas were able to achieve high body masses while actively molting the flight and contour feathers (Koopman 1986). The data for several shorebird species studied on the Banc d'Arguin during their preparation for northward flights (Zwarts et al. 1990c), that for Ruffs preparing for a southbound flight (Koopman 1986), and that for Bar-tailed Godwits staging in the Wadden Sea *en route* to their subarctic breeding grounds (Fig. 6) suggest that nutrient storage and feather production are compatible under some circumstances. The basis for the differences remains unknown.

WHAT ARE THE ROLES OF TIME, ENERGY AND NUTRIENTS?

To reach the subarctic breeding grounds in time, Bar-tailed Godwits clearly operate under time constraints (Piersma 1987, Drent and Piersma 1990, Piersma and Jukema 1990). Individuals unable to reach a body mass of 400 g (males) or 480 g (females) by 1 June are unlikely to reach the breeding grounds in time or with sufficient nutrient reserves (Piersma 1987). Godwits therefore must ensure that nutrient storage conforms to a 'migration schedule' that specifies the timing and patterning of flights necessary to complete a migration leading to successful reproduction (Piersma and Ens 1992).

Individuals unable to keep to schedule apparently forego the possibility to improve the quality of the breeding plumage on the last staging site (Fig. 6). That such individuals have breeding plumages that are less complete than that of birds which do molt suggests that the delays in schedule may already have occurred during migratory preparations in West Africa. Energy storage and molt are thus compatible only if individuals are sufficiently heavy for the time of the year, suggesting that nutritional trade-off criteria are set with reference to an endogenous representation of an 'optimal' migration schedule.

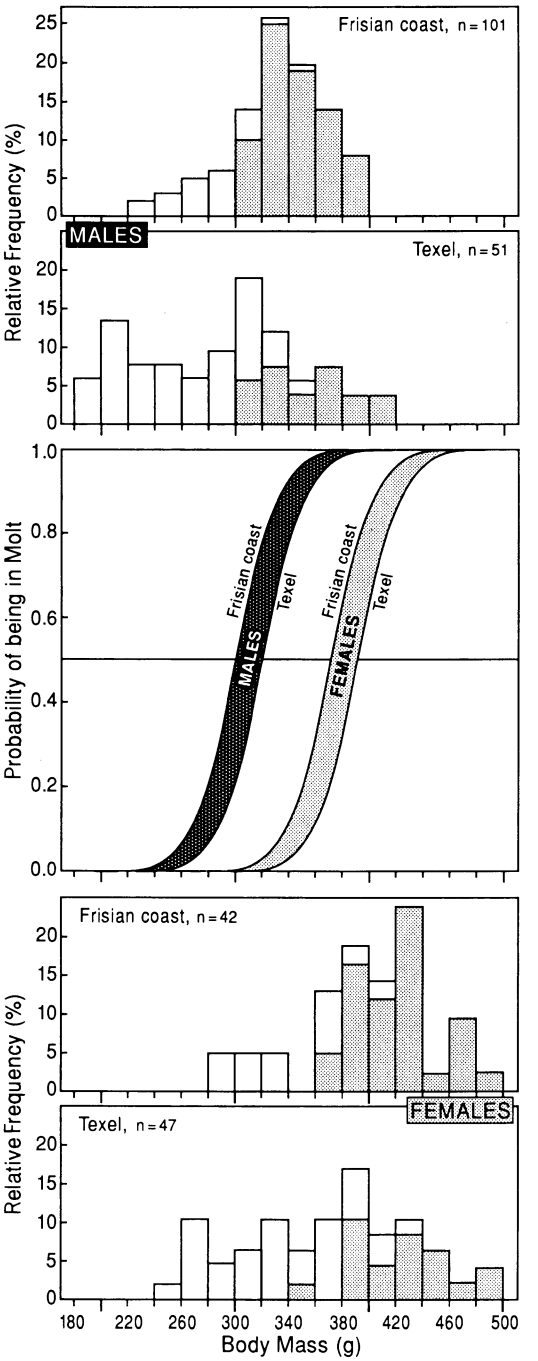

FIGURE 7. Contour feather molt as a function of body mass in male and female Bar-tailed Godwits at two staging sites in the Dutch Wadden Sea in the period 18–22 May. In the top two panels the frequency distributions of body mass of males which are in molt (shaded) or not (open histograms) at either the Frisian coast or on Texel are presented, and the same is given for females in the lower two panels. The mid-panel give the logistic regression functions of the probability of being in molt conditional upon body mass for the four different categories of birds (see text and Table 4 for the details of this model).

TABLE 4. Logistic regression models for the probability of Bar-tailed Godwits (of different body masses, of two sexes and from two sites: Frisian coast and Texel) of being in molt (p) in the period 18–22 May (n = 241). To evaluate the different models we give the deviance (D), degrees-of-freedom (df), difference in deviance (G^2), difference in degrees-of-freedom (v) and significance compared to the model with all main effects (model 2). The logit model with all main effects is given by logit (p) = $-21.79 - 5.216 \cdot \text{sex} - 1.368 \cdot \text{site} + 0.07164 \cdot \text{mass}$, where sex is either 0 (=male) or 1 (=female) and site is either 0 (=Texel) or 1 (=Frisian coast). The data and the model are presented in Figure 7.

Model		D	df	G^2	v	P
Null model	(most simple model: constant probability p)	325.6	240			
Model 1	main effects except one:					
	minus body mass	286.9	238	154.6	1	<0.001
	minus sex	193.9	238	61.6	1	<0.001
	minus site	141.4	238	9.1	1	<0.001
Model 2	all main effects	132.3	237			
Model 3	all main effects plus all two- and three-way interactions	128.3	231	4.0	9	N.S.
Full model	(most complex model)	0	0			

Since a migration schedule is comprised of time, energy and nutrients, we formulate three non-exclusive hypotheses to explain the absence of contour feather molt in some staging godwits.

1) Time. Godwits that do not molt are those that arrive too late in the Dutch Wadden Sea to complete contour feather molt before the flight to the breeding grounds.

2) Energy. Godwits which are too light for the time of the year forego molt because the energy requirements of molt compete with those of energy storage needed to acquire the 'optimal' take-off mass. (This hypothesis has a time component).

3) Nutrients. Since the production of rusty-red contour feathers necessitates a critical and uncommon specific nutrient, only very proficient foragers are able to afford a molt on the staging areas. These individuals will usually be heavy for the time of the year.

Flying long-distances apparently is not compatible with molting contour or flight feathers. If the population of Bar-tailed Godwits were to leave the Wadden Sea on 1 June (the average date), and if the molt duration was about 12 days, then we would expect to find no individuals starting the molt (phase 1) from about 12 days before 1 June. This is what we found (Fig. 3). However, the same hypothesis would predict that before 20 May all birds would be molting. This is not the case (Fig. 3). Thus, energy and nutrients may partially explain individual differences in the occurrence of molt.

During all of May, non-molting godwits weigh less than molting birds, suggesting that non-molters must concentrate on storing more nutrients at the cost of molting contour feathers. We have no data on feeding rates in molting and non-molting individuals, so the energy/nutrients competition for storage and molt hypothesis can only be explored by comparing the average daily requirements of molt with those of energy/nutrient storage. Godwits produce 0.09 g (females) to 0.13 (males) of feather material per day in a period of about 12 days. During their staging period in the Wadden Sea, males increase in mass at an average rate of 5.65 g/day and females with 7.52 g/day (Piersma and Jukema 1990). About 35% of this mass increase consists of wet protein (Lindström and Piersma 1993), with an average energetic density of 6 kJ/g. The remainder consists of fat with an energetic density of 39 kJ/g. Assuming a deposition efficiency of 80% (average of values reported by Ricklefs 1974 and Kersten and Piersma 1987), the energy requirement of 5.65 g/day stored by males is thus equivalent to $((0.35 \times 5.65 \times 6) + (0.65 \times 5.65 \times 39))/0.8 = 226$ kJ/day. Assuming that the production cost of dry feather tissue Bar-tailed Godwits is the same as in Kestrels *Falco tinnunculus* (117 kJ/g, Dietz et al. 1992), the feather production cost of molting male godwits in the Wadden Sea would average 15 kJ/day. This equals 7% of the cost of energy storage and 6% of the total production costs of molting males. Birds with equal daily energy intake rates would thus trade a 15/(226/

5.65) = 0.4 g/day mass increase against the contour feather molt, yielding a total difference in storage potential of 12 × 0.4 = 5 g over the molt period. Although 5 g energy stores obtained by foregoing molt may seem trivial for 400–500 g birds, we do not know the rates and constraints on the daily intake faced by the godwits.

There is, however, another indication that nutritional/resource factors play a role. Between 18 and 22 May 1992, birds of either sex staging on Texel had a lower average body mass than birds staging along the Frisian coast in earlier years, and yet only molted when having attained higher body masses. Since the feeding conditions for Bar-tailed Godwits in May 1992 on Texel were not good relative to other years and sites (L. Zwarts and A.-M. Blomert, pers. comm.), this suggests that the threshold mass to start molt on the staging grounds is set with reference to the current and expected foraging revenues. Feeding longer or harder may have a significant fitness cost (see Metcalfe & Furness 1984) and the variation in threshold mass thus indicates the importance of nutritional factors.

We have no evidence that production of the rusty-red breeding plumage feathers requires a particular, diet-specific nutrient, as it does in some birds (e.g., Hill 1992). Bar-tailed Godwits feed on a wide variety of invertebrate foods, with individuals apparently temporarily specializing during their staging period in the Wadden Sea (Piersma et al. MS). However, there is no evidence for relationships with the occurrence of molt. Red Knots (*Calidris canutus*) produce a breeding plumage of a color indistinguishable from that of the godwits, and continue to do so on a monotonous diet of trout food pellets (T. Piersma, unpubl. data). We conclude that Bar-tailed Godwits are likely to decide on the basis of time as well as on nutritional factors.

ADAPTIVE ASPECTS OF THE MOLT INTO A RED BREEDING PLUMAGE

The overall change in color from greyish in winter to rusty-red during spring staging makes godwits on tidal flats more conspicuous to human observers. Although the rusty-red plumage may be adaptive for reasons of camouflage near the nest, no comparative data are available to support this. Males, which are more numerous than females and possibly subject to the strongest sexual selection, show the most intense plumage color and are thus most conspicuous. Similar to other bird species (e.g., Rohwer 1977, Edwards 1982, Lyon and Montgomerie 1986), the red plumage of godwits might play a role in the establishment of breeding territories and during pair formation.

Why do the godwits grow a striped feather during the transition from a winter to a breeding plumage (Fig. 3)? In temperate-wintering Bar-tailed Godwits, striped feathers are first produced in January (J. Jukema, pers. obs.). This conforms with Boere's (1976) observation that Bar-tailed Godwits show some contour feather molt throughout the winter. The intensity of the rosy background color of the striped feathers appears to increase with date of appearance until only evenly red and unstriped feathers are produced (J. Jukema, pers. obs). The functional significance of this pattern eludes us.

PLUMAGE COLOR AS AN HONEST SIGNAL FOR MIGRATORY QUALITY

If godwits with the most complete breeding plumage can still improve the quality of this plumage by growing fresh contour feathers on the last staging site before the breeding grounds, and if this category also consists of relatively heavy individuals at a time of the year when the amount of stored nutrients counts, it is likely that the quality of the plumage upon arrival on the breeding grounds indicates migratory quality. Migratory quality indicates the capability of individuals to perform on time. This would be important if seasonally early individuals have a reproductive advantage over later birds (e.g., Perrins 1965, Daan et al. 1990). If the reddest birds are the best migrants, plumage color and quality may provide godwits with an indicator to judge potential mates' migratory skills other than on the basis of arrival time and fatness. This implies that migratory skills have a genetic basis. However, high quality plumage could also be a condition-dependent handicap revealing that an individual does not presently face nutritional stress and has therefore a greater potential to be a good parent. High quality migrating and molting performance would then be only a characteristic of a given bird in a given year. This hypothesis does not require migratory skills to have a hereditary component. Data on the repeatability between years of date-dependent body mass, molt phase, and plumage score could help differentiate between these hypotheses and also elucidate whether age effects are important.

Whatever the genetic basis, the extent and quality of the breeding plumage might allow potential partners to evaluate each other's annual performance. This view was anticipated by Murton and Westwood (1977, p. 498): "we wonder whether . . . females selecting males on the basis of specific plumage traits could select for an advantageous physiology." It remains to be shown that the nutritional costs of the molt relative to the other demanding physiological tasks faced by long-distance migrants before the breeding season are great enough to inhibit "cheating" (Hill 1990).

Most arctic-breeding shorebirds change notably in plumage with the advent of the migration to the breeding grounds. That the most northerly breeding populations of Greater Golden Plovers (*Pluvialis apricaria*) and Dunlins (*Calidris alpina*) also show the greatest change from winter to breeding plumage, as indicated by the extent of black on breast and belly (Cramp and Simmons 1983), may relate to mate choice in long-distance migrants if they use plumage cues to judge migratory quality. Studies of mate choice and sexual selection in a range of shorebird species are needed to test this. That individuals of the long-distance migrant Pied Flycatcher (*Ficedula hypoleuca*) with the least conspicuous breeding plumage arrive latest on the breeding areas (Slagsvold and Lifjeld 1988) and may therefore face a mating disadvantage (Lundberg and Alatalo 1992), suggests a similar interaction between migration, molt and mate choice.

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